BEHAVIOR, ECOLOGY, AND CONSERVATION OF MOUNTAIN LIONS IN FRAGMENTED HABITAT

John W. Laundre', Mike Sellers, Tim Clark[1], and Donald P. Streubel

Department of Biological Sciences, Idaho State University

Pocatello, ID 83209

[1]Concurrent with Northern Rockies Conservation Cooperative, Box 2705, Jackson, WY

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A progress report

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Prepared by:

John W. Laundre', Mike Sellers, Tim Clark[1], and Donald P. Streubel

Department of Biological Sciences

Idaho State University

Pocatello, ID 83209

[1]Concurrent with Northern Rockies Conservation Cooperative, Box 2705, Jackson, WY 83001

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INTRODUCTION

The mountain lion (Felis concolor) once ranged from northern British Columbia to Argentina (Young and Goldman 1946). Today, in North America, this species is restricted to the western one third of the country, with a small population in Florida (Russell 1978). This major reduction in range resulted from habitat fragmentation and loss coupled with past campaigns to exterminate the species.

As habitat becomes fragmented, animals are restricted to ever shrinking "islands" of appropriate habitat and lose critical corridors used to travel between these islands. Mountain lions, individuals and populations, become isolated from each other, resulting in reductions in effective population size and genetic diversity. These reductions, in turn, increase the possibility of local extinctions and further reductions in the range of mountain lions. As human populations and subsequent habitat fragmentation and loss increase, it is imperative that we gain as much knowledge as possible about mountain lion behavior and ecology. To date, several investigators have studied various aspects of mountain lion behavior and ecology (Hornocker 1969, Seidensticker et. al 1973, Neal et. al 1987). However, these studies, as well as others, were of lions in large areas of contiguous habitat. Knowledge of mountain lion behavior and ecology in fragmented habitat is lacking.

Our study is designed to collect data on the behavior and ecology of lions living in an area of extensive fragmentation. Our specific objectives are to 1) document activity and home range use patterns, 2) document basic population dynamics, 3) investigate predator-prey interactions, and 4) develop a viable conservation management plan for lions living in fragmented habitat. Work on this project is scheduled to continue for the next several years. This report summarizes research efforts up to June 1990.

STUDY AREA

The study area is in southcentral Idaho and northwestern Utah (Fig. 1). This area occupies approximately 2,500 km^2 and is composed of small isolated mountain ranges (approximately 1,000 km^2) (Fig. 2) separated by agricultural valleys. The City of Rocks National Reserve is located within the study area. In 1989 the reserve received 45,000 visitors (David Pugh, Personal communication). This number is likely to increase over the next few years along with subsequent development of facilities to accommodate the increased use. A large gold mining operation is also under development in the Black Pine Mountains. All of the mountain ranges in the study area are easily accessable by four wheel drive vehicles and on horseback.

METHODS

Fulfilling most of our objectives depends on capturing and radio-collaring of lions in the winter. When mountain lion tracks are located, trained hounds are used to chase the animal until treed. Once treed, the animal is immobilized with a mixture of Ketamine (10.0 mg/kg) and Rompun (0.2 mg/kg) via a Cap-chur^R gun. Immobilized mountain lions are measured, weighed, and sexed. Age is determined

Figure 1. Location of study area in southcentral Idaho and northwestern Utah.

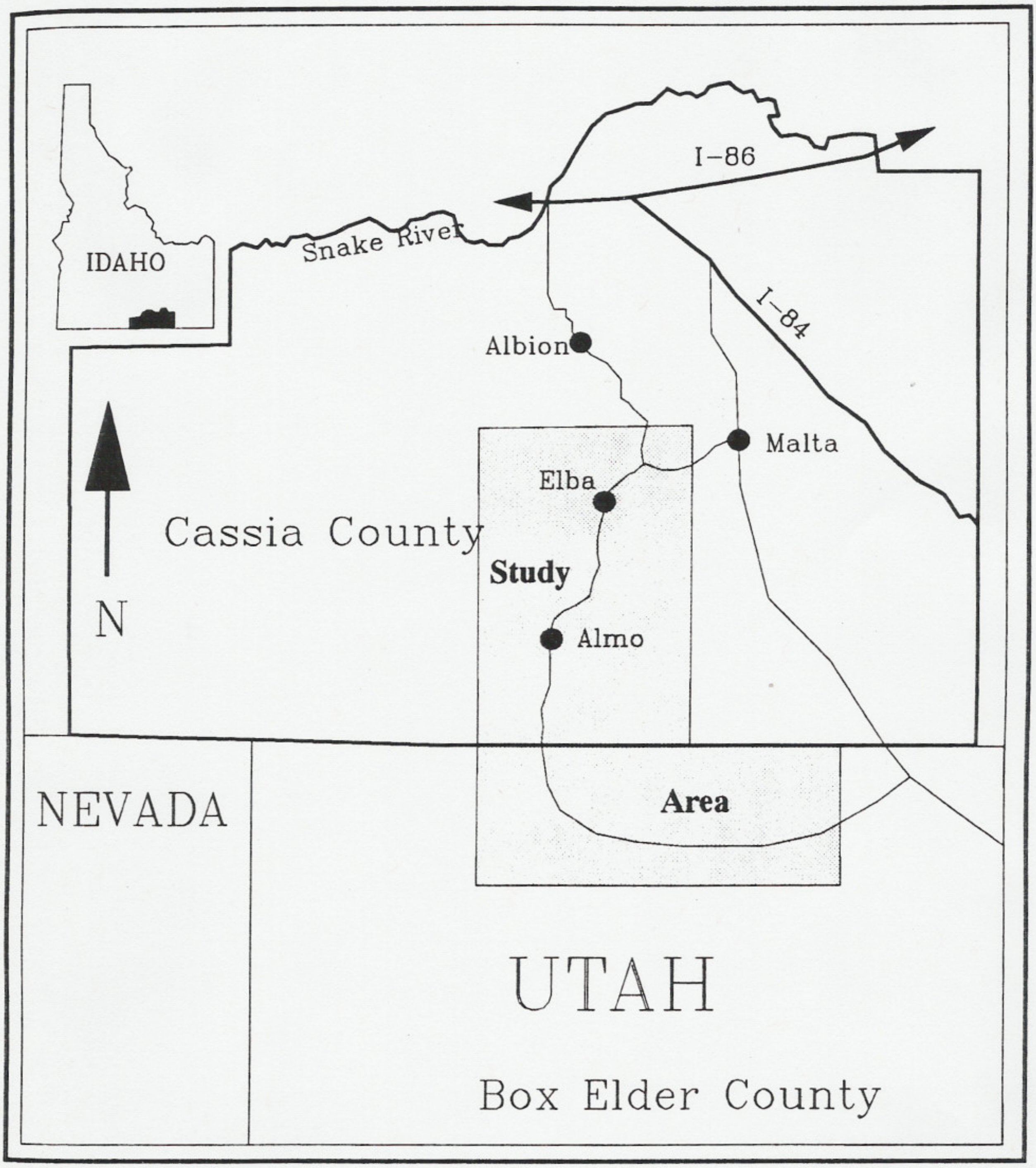
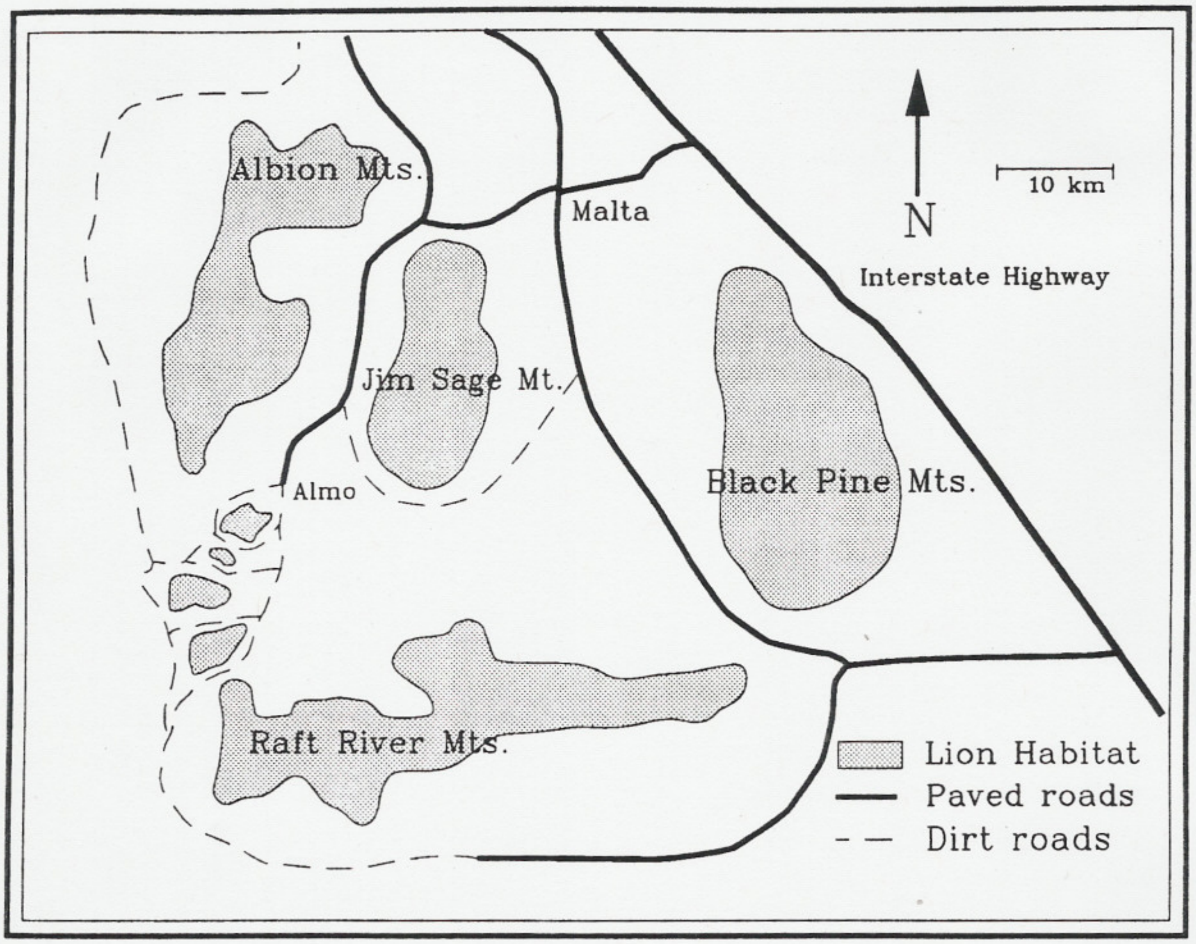


Figure 2. Schematic overview of the study area, showing juxtaposition of the various small mountain ranges.



by dental characteristics (Shaw 1983). Each mountain lion is then ear-tattooed and fitted with a radio collar, some of which are equipped with an activity sensor. The activity sensor switches between two different pulse frequencies depending on the position of the animal's head. Tranquilized mountain lions are observed until they recover and escape.

Home range use and activity:

To determine home range characteristics, collared mountain lions are relocated by radiotelemetry. Point locations (Laundre' et al. 1987) on mountain lions are made with a hand held yagi antenna a minimum of once per week. Sequential relocations (Laundre' et al. 1987) are collected during 24 hour monitoring periods in the summer with help from Earthwatch volunteers. During these monitoring periods two double yagi null/peak systems are set up at appropriate locations and simultaneous compass bearings are taken at half hour intervals. Point locations are used to ascertain home range size, whereas the sequential locations are used to determine home range use patterns and activity.

Home range size was determined by use of the grid method (Rongstad and Tester 1969). For the purpose of this report, a one km^2 grid cell system was used. Home range size was initially estimated to equal the number of grid cells in which radio fixes were recorded. Additional grid cells in which their logical inclusion was obvious, were added to the total to give a better estimation of home range size (MacDonald et. al 1980). The size of the grid cell used in the future will depend on the accuracy of the telemetry system. The main null hypothesis to be tested is that home range sizes of lions from this study do not differ from those of lions living in unfragmented habitat. A secondary hypothesis of similar home range sizes between males and females will also be tested.

Home range use patterns were estimated based on the percent time an animal spent in various grid cells of its home range while it was monitored. The grid cells of the home range were superimposed on a habitat map of the area to determine habitat use patterns. The main null hypothesis to be tested regarding habitat use is that an animal uses the different habitat types of its home range in the same proportion as the habitats' occurrence.

Concurrent with the 24-hour monitoring periods, lion activity was assessed by recording the number of pulse frequency changes a transmitter made per hour and by estimating the distance an animal moved per hour. For pulse frequency changes, the assumption is that an active animal will move it's head more often than a sedentary one and result in a higher number of pulse changes per unit time. It is further assumed that the number of pulse changes per unit time is related to the degree of activity in a predictable manner. This assumption is currently being tested by regressing the pulse frequency change rate with the distance an animal moved per hour. The distance an animal moved per hour was estimated by measuring the straight line distance an animal moved between successive half hour relocations.

Population Dynamics:

Data on the population dynamics of lions in the study area come from a variety of sources. Estimations of lion population size for the study area are based on reports of hunter killed lions, capture data from our pursuit efforts, systematic searches for lion sign in the winter, and reports of sign or lions from local houndsmen. Lion hunters who harvest a lion must check the carcass in with either the Idaho Department of Fish and Game or the Utah Division of Wildlife. Records of these animals are then forwarded to us by personnel in these agencies. The study area is intensively searched during the winter months to locate lion tracks. Roads separating islands of lion habitat are systematically driven when snow conditions are favorable. Locations of lion tracks crossing these roads are noted on a map. Tracks found are measured and recorded as to being single or multiple (female with kittens). Additionally, selected areas of lion habitat are searched on foot and lion sign is recorded. Occasionally, local lion hunters report lions or lion sign they have found to us. The reliability of these reports varies with the individual. If possible, the reports are followed up with on site visits to the areas. All these data are used to develop estimates of population size for each winter of the study. Population density of lions will be calculated based on the amount of usable habitat rather than total study area size.

The age of captured lions is estimated by tooth wear and gum recession (Shaw 1983). When possible, teeth from hunter killed lions are collected and dental annulations (Thomas and Bandy 1973) used to age these animals. Age determination from teeth is being made by Matson's Laboratory, Milltown, Montana.

The data on hunter killed lions and the fate of radio-tagged individuals are used to develop mortality patterns for the population. Unmarked lions, especially kittens, known to be in the area one winter but which are not found the next winter, are presumed to have died or emigrated.

The data on population size, density and survival will be used primarily to characterize the population and for modelling. Comparison of our findings with those of other studies will be made but no statistical comparisons are anticipated.

The genetic relationships of the lions in the study area are being determined by electrophoretic analysis. Blood samples are collected from lions when they are captured. These samples are sent to the National Cancer Institute, Fredricksburg, Maryland for analysis. Results of the analyses will be used to determine the degree of genetic relativeness of the lions in the population.

Predator-prey relationships:

Data are being collected on mule deer killed by lions during the winter months. Lion kills are found by searching winter ranges of deer and following lion tracks. Once found, the deer carcasses are aged, sexed, and the nutritional condition of the animals is determined by examining their bone marrow. Ages of the deer are being determined by microsectioning one of the first incisors (I1) and counting dental annulations (Thomas and Bandy 1973). Age determinations are being made by Matson's Laboratory, Milltown, Montana. Percent fat of the bone marrow is initially classified relative to structure and color (Cheatum 1949). White, waxy marrow indicates a deer in healthy condition; red, gelatinous marrow indicates an animal in poor nutritional state. Marrow samples are sealed in plastic bags and percent fat content is later estimated by the reagent dry technique described by Verme and Holland (1973).

Data are not available on the age/sex structure or health state of the deer herd in the study area. Thus, no statistical comparisons of our data to the general population can be made. If there are sufficient data on age, sex, and nutritional state of deer known to be killed by male and female lions, unpaired t-tests between deer killed by male verses female lions will be conducted. Characteristics of the deer to be compared between sexes of lions would be average age and nutritional state (percent fat). The null hypothesis of interest would be no difference in the mean of the characteristic being tested between deer killed by male and female lions.

Sites where deer are killed by lions and where deer bed down for the night are marked in the winter. These sites are relocated in the summer and vegetation and topographic characteristics of the areas are measured. Vegetative characteristics of sites are quantified by the point-quarter method as outlined in Brower and Zar (1977). Point quarter samples are taken at the approximate site where the lion attacked the deer, as determined by tracks in the snow, and where the lion cached the carcass. Sixteen additional samples are taken at predetermined points within a 50 x 50 m grid centered around the kill site. The point-quarter sample from the kill site is used as one estimate each of tree and shrub density, tree diameter, and shrub height for the area. The average of the sixteen "general area" samples is used as a second estimate. The kill site and general area estimates for all kill sites will be compared with a paired-t test to determine if vegetation of the kill site differs from the surrounding area. The null hypothesis to be tested is the difference between kill site and general point estimates for the tested characteristic is zero.

Deer bed sites are usually found in groups of five or more. Point-quarter samples are taken at each bed site. Sixteen additional samples are taken in a 50 x 50 m grid encompassing the bed sites. Tree and brush density, tree diameter, and shrub height estimates at the bed sites within an area are statistically compared to the estimates from the general points within the area with a group-t test. The null hypothesis is the difference between means of the characteristic being tested from the bed sites and general points is zero. Vegetative characteristics of deer bed sites from different locations in the study area are being compared with a single factor analysis of variance to determine if bed site characteristics differ among locations. The null hypotheses tested are the means of the characteristic being tested among locations do not differ.

Topographic features measured at kill and bed sites include slope, aspect, and roughness. Slope is measured through the kill site/deer bed with a hand help clinometer. General aspect is measured with a compass. Roughness (Whitfield 1983) is estimated by measuring degree slope at four points, each 50 m from the kill/deer bed. Two points are right and left of the sample point and perpendicular to the slope and two points are up and down slope from the point. The roughness index is the square root of the summed deviations of the four slope readings from the slope at the sample point and range from 0 to 180^0. Topographic measurements for each kill site/deer bed will be used primarily to characterize the areas and to statistically compare these sites to the general characteristics of the study area on a large scale.

On a larger scale, the general vegetative/topographic characteristics of kill sites and deer bed sites will be classified based on data from Geographic Information System (GIS) files. The percent occurrence of kill sites and bed sites in different vegetative and topographic types will be compared to the percent occurrence of those types in the study area. This comparison will determine if predation success by lions and bed selection by deer show a preference for certain characteristics.

RESULTS

Capture success

Winter weather patterns in the west are characteristically cyclic with years of heavy snow fall followed by drier years. The last years of abundant winter snow were between 1979-84. Since then winter snow conditions became increasingly dryer with the winter of 1986-87 being the driest year of the cycle. Little snow fell and generally remained on the ground for only a few hours. Finding fresh lion tracks was difficult, in part because deer did not concentrate on traditional winter ranges and lions remained widely spread over the entire study area. Lion numbers in our study area were also found to be quite low (See section on population estimates). Snow conditions in the winters of 1987-88, 88-89, and 89-90 were slightly better than the first year but still below average. Given the poor snow conditions and the low lion densities we were still able to tree 10 lions during the four winters (Table 1). Seven of the lions were adults (four females, three males) and three were kittens (two females, one male). All the adults were fitted with radio collars and then released. One of the kittens was fitted with an expanding radio collar while the other two were only eartagged.

Home range size and use

We have adequate data on home range size for four adults (two females and two males) (Table 1). The females, Lady and Lola, had home ranges of approximately 80 km^2. Both their home ranges consisted of a southern and a northern part. For Lola, locations, either radio fixes or captures, were made in 44

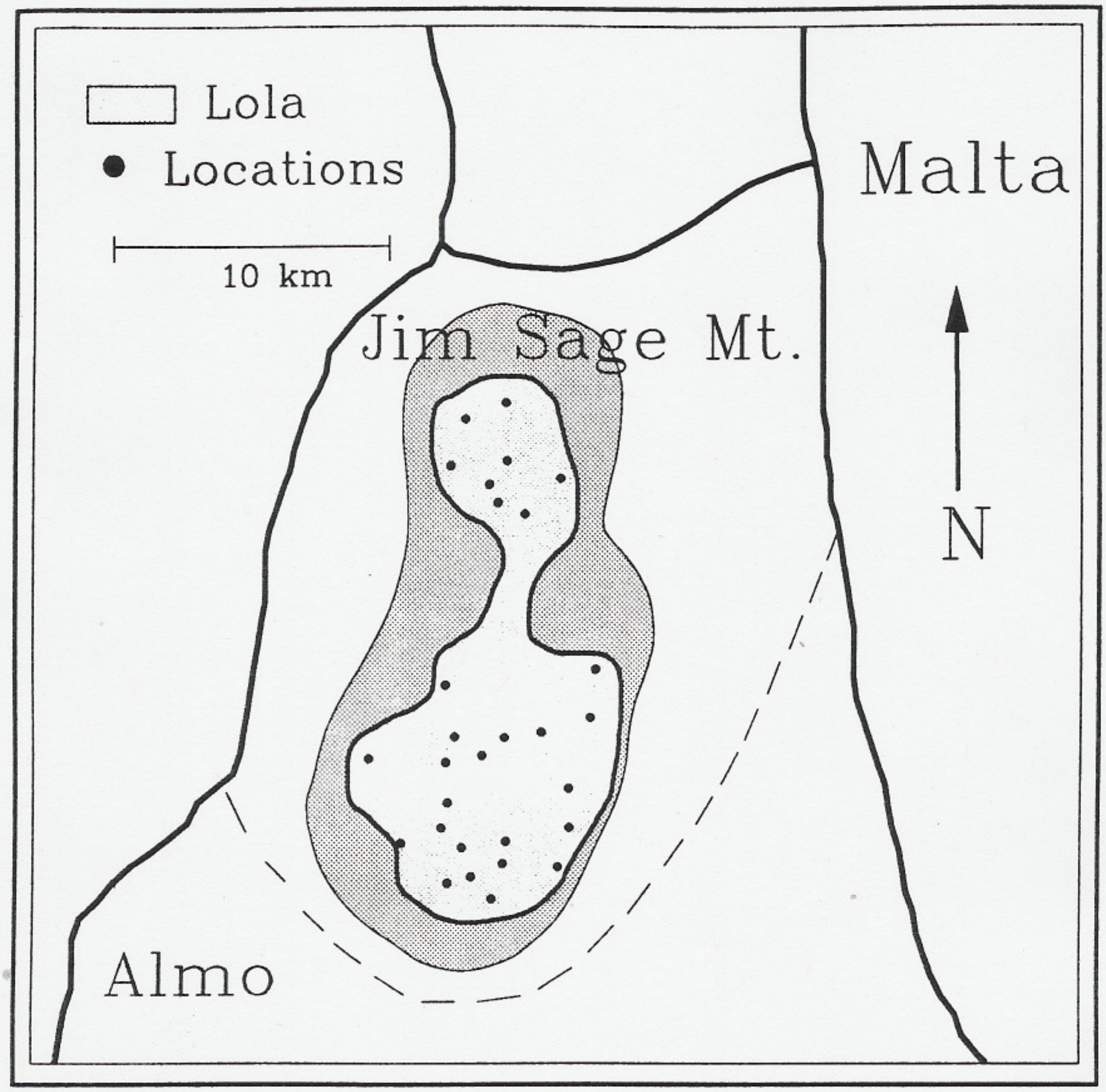
Table 1. Summary of data for mountain lions captured as of June 1990.

Lion	Date Captured	Sex	Age	Weight	Last Located	Total # Locations	Home range size
Lady	1/7/87	female	1-2 years	45 kg	8/2/87	31	74 km^2
Lola	1/7/88	female	4+ years	50 kg	8/14/90	100	80 km^2
Trixie	12/28/88	female	kitten	10 kg	2/26/89	NA	NA
Wanda	12/28/88	female	kitten	8 kg	4/2/89	5	NA
Ruby	12/1/88	female	<2 years	38 kg	12/22/88	6	NA
Butch	4/2/89	male	2+ years	59 kg	1/23/90	40	230 km^2
Sheila	1/7/89	female	3+ years	50 kg	1/13/89	2	NA
Spike	1/12/90	male	kitten	16 kg	1/19/90	2	NA
Duke	1/4/90	male	<2 years	50 kg	1/15/91	5	NA
Bill	1/15/90	male	5+ years	64 kg	12/8/91	40	49 km^2

grid cells in the southern portion and 18 in the northern of her home range (Fig. 3). No locations were made in the area between the northern and southern portions of her range. She apparently uses the middle portion of the range only for travel. Based on field observations, seven more grids may be added to give a total home range area of 80 km^2.

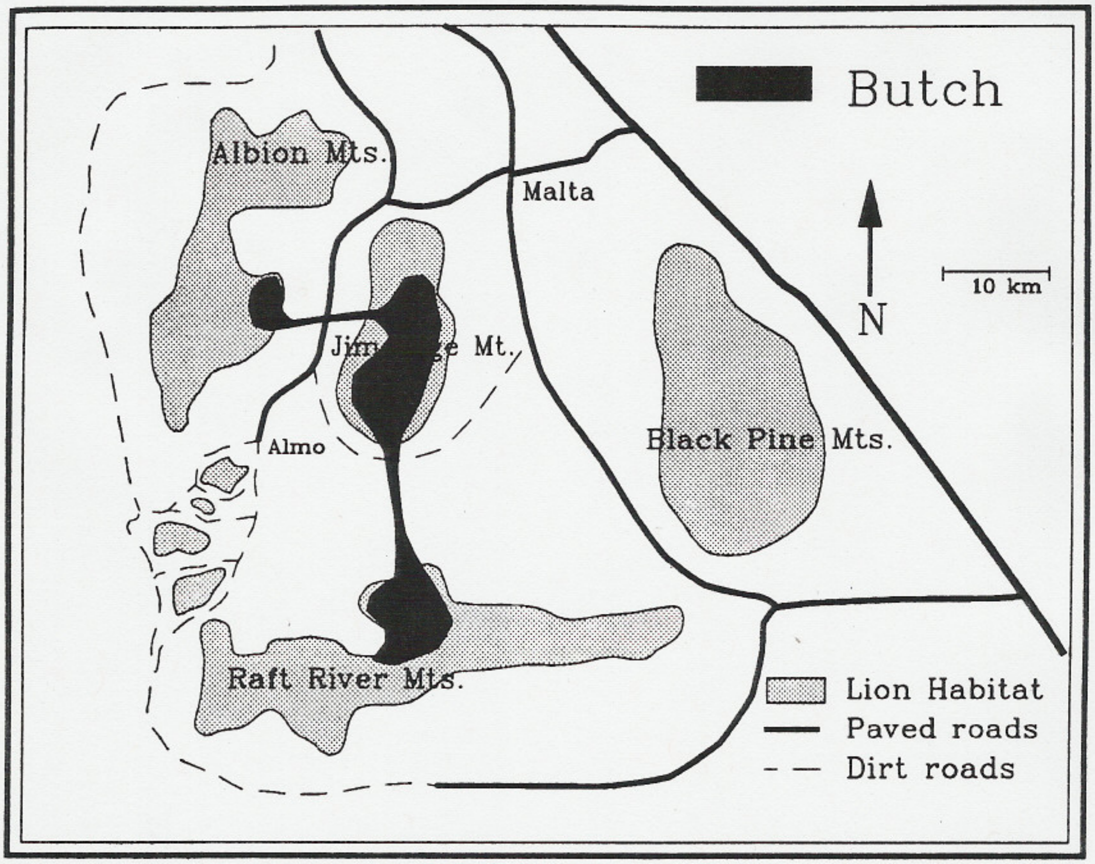
One male, Butch, had a home range that included three mountain ranges and spanned two states (Fig. 4). His home range encompassed 230 km^2, including the corridors he used when traveling between these ranges. The other male, Bill, remained in a relatively small (49 km^2) and rugged area of the Albion Mountains.

Figure 3. Home range area of the adult female Lola.



For the females, home range use during the winter was restricted to relatively small areas that were known to have wintering deer. As spring approached, these animals increased their area of use and made major movements to other portions of their range. The two males, however, traveled more extensively throughout their ranges during all times of the year.

Figure 4. Home range area for the adult male, Butch.

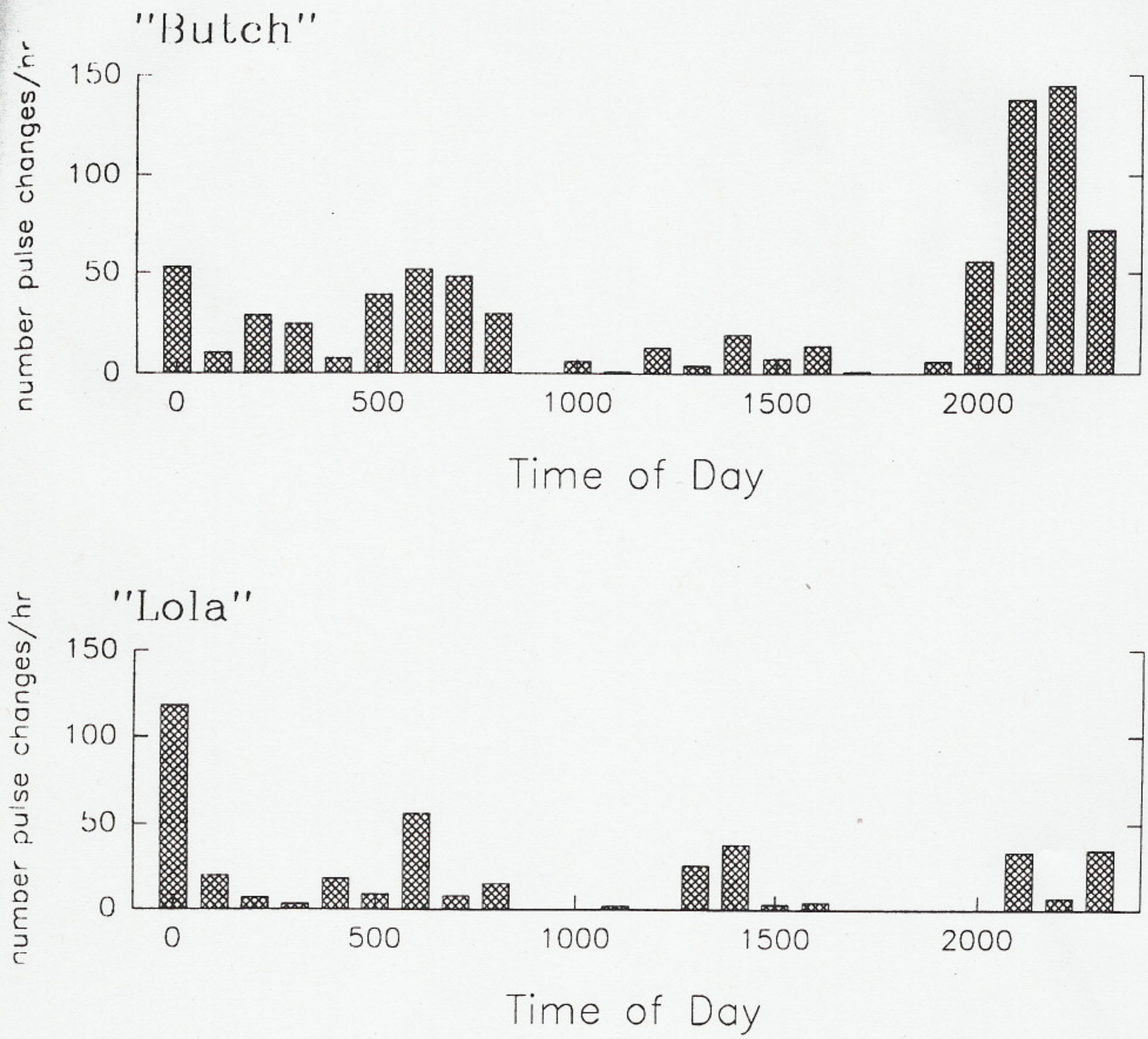


Analysis of habitat use patterns is still in progress and no quantitative assessment can be made at this time. Qualitatively, lions seem to spend most of their time in the patches of wooded habitat that contain rock outcrops. Lions spend very little time in open sage-grass areas, only moving through them quickly between forested patches.

Activity

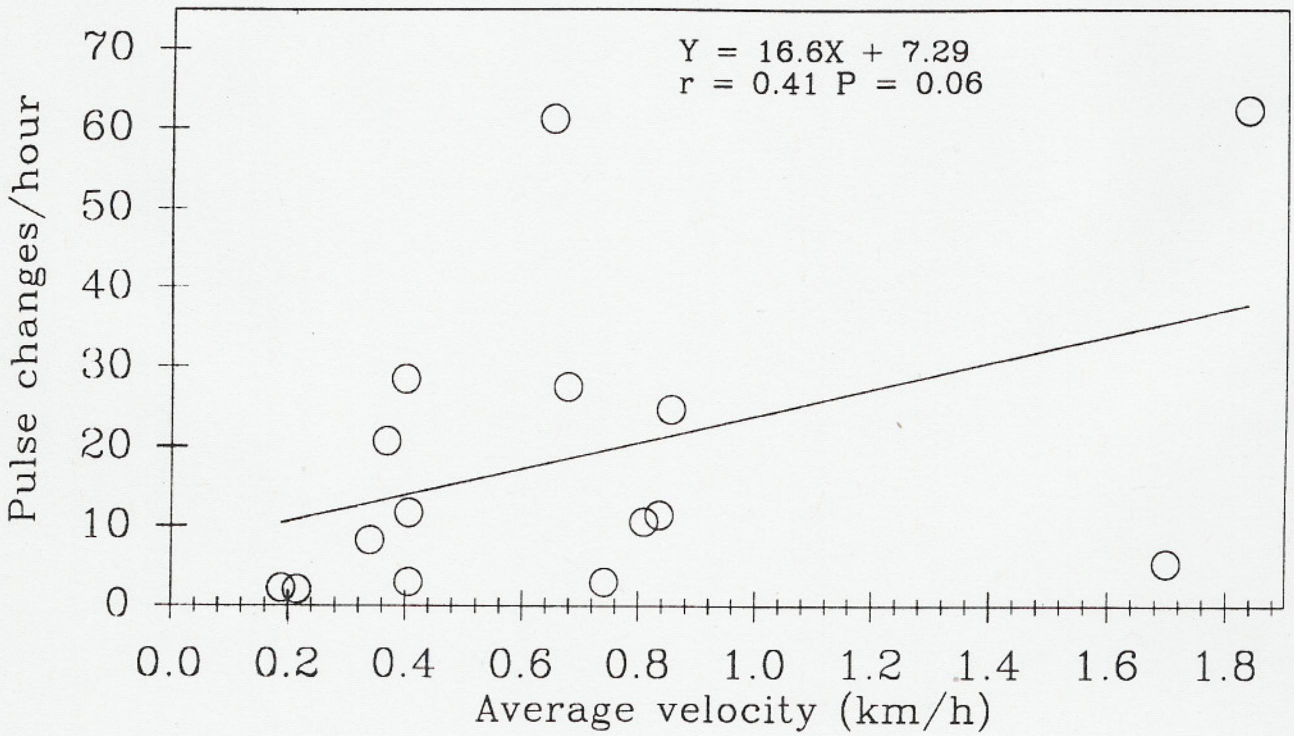
Generally, summer activity was restricted to evening hours, characterized by two or three active periods per night (Fig. 5). Animals remained inactive during the day, often "holing up" in the rocks causing the loss of their radio signal for several

Figure 5. Example of summer activity cycles, based on number of pulse changes, for the adult female, Lola and the male Butch.



hours per day. They then became active again with the onset of evening. Often, animals had a minor peak of activity around noon; possibly to avoid the hot sun. Although there was a positive regression between distance moved/hour and pulse changes/hour (Fig. 6), for the purposes of this paper, activity is defined as the times when the mountain lions are moving around and should not be confused with distances moved. Based on available data, activity patterns do not seem to vary between males and females.

Figure 6. Regression of the number of pulse frequency changes per hour against distance moved per hour for Lola and Butch.



The data on distance moved are still being analyzed. The adult female, Lola, was monitored for twenty hours in September, 1988. During this period she moved 9.03 km at an average velocity of 0.45 km/hr. The elevations she used ranged between 1,877 and 2,079 m. At this time, it is unknown if this movement pattern is typical. Qualitatively, lions seem to exhibit two general movement patterns. At times, lions confined their movements during a 24-hour period to a relatively small area. At other times, an animal would move extensively within its home range. Further analysis of the data should clarify these patterns.

Interactions with conspecifics

Simultaneous monitoring of collared animals enabled delineation of several conspecific interactions. During the end of January a fresh deer kill was located in the southwest portion of Lola's range. Based on the size of the lion track it was determined that the female did not make the kill. At that time, Lola suddenly moved to the northeastern end of her range, presumably in response to the presence of the other lion.

Based on six locations, Lola and her kittens were together 50 percent of the time. Distance between Lola and her kittens was as much as 4.0 km. The average distance between Lola and her kittens was 0.9 km.

On April 2, 1989 Lola's kitten, Wanda, was killed by a male mountain lion. The kitten was not cannibalized. The male (Butch) was pursued and collared near the location where the kitten was found. Two attempts were made to locate the other kitten, however she was never found. On April 24, 1989 Lola and Butch were located together on the southwest end of the Jim Sage Range and presumably mated.

Lion predation

As of June, 1990, 17 mule deer killed by lions have been located. They include males and females, adults and juveniles, and animals in good and poor condition (Table 2). The kill sites have been marked and during the 1988-89 field season, vegetative parameters surrounding five sites were measured (Table 3). The mean

Table 2. Summary of deer killed by lions.

Date Found	Sex	Age	Condition Texture	Color	% Fat[a]	Lion
12/11/85	M	Ad	Gel	Pink	1.5	?
12/12/85	F	Ad	Wax	White	90	?
12/12/85	M	Ad	Gel	Red	1.5	?
12/15/85	M	Fw	Gel	Red	1.5	?
12/18/87	M	Ad	?	?		?
12/23/87	F	Ad	Wax	White	90	?
11/19/88	M	Ad	Wax	Pink	85	Lola
1/4/89	M	Fw	Gel	Red	1.5	?
2/8/89	F	Ad	Gel	Pink	1.5	?
2/8/89	M	Fw	Wax	White	90	?
1/3/90	F	Ad	Wax	Pink	85	?
1/19/90	F	Ad	Wax	White	90	Lola
2/6/90	M	Ad	Wax	White	90	?
2/6/90	M	Ad	Wax	White	90	?
2/15/90	?	Fw	Wax	Red	70	Female #5
2/28/90	M	Fw	Wax	Pink	85	Bill
2/21/90	F	Ad	Wax	Red	70	Female #5

[a]Based on scale developed by Cheatum (1949)

distance between trees at the kill sites averaged 9.8 m or a tree density of 104.1 trees per hectare. Shrub density was estimated to be $0.14/m^2$.

Table 3. Vegetative and topographic analysis of lion kill sites.

	Date of Kill	Tree Data Dist.	DBH	Shrub Data Dist.	Height	Topography Slope	Aspect
1-85	12/11/85	12.1	3.2	1.3	0.30	-	220^0
1-89	1/4/89	14.8	9.1	1.1	0.18	23^0	170^0
2-89	11/19/88	12.8	6.0	1.4	0.37	13^0	290^0
3-89	2/8/89	5.2	1.3	7.2	0.52	26^0	190^0
4-89	2/8/89	4.3	7.2	2.3	0.27	22^0	225^0

Deer Bed Analysis

To date, 72 deer bed sites in eight areas have been sampled for vegetative and topographic features. The data for four of the areas are summarized in Table 4. Significant differences among areas were found for tree distance, tree diameter, shrub height, and slope. Analysis of the remaining four areas should add significantly to our understanding of the types of areas deer select to bed in.

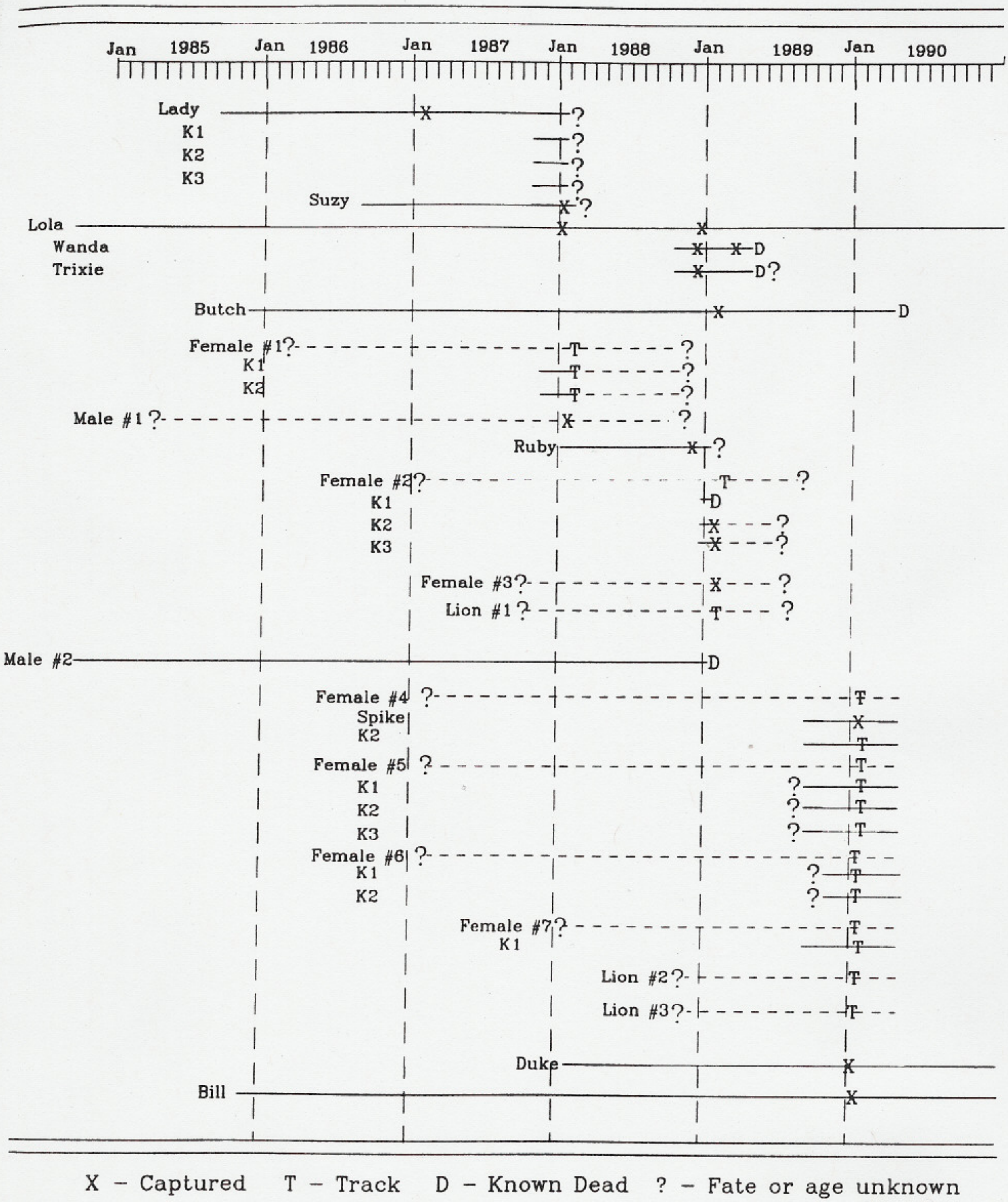
Table 4. Means±SE of vegetative and topographic characteristics of deer bed sites. Means within a column with the same letter were statistically similar.

Area n	Tree dist.	Tree DBH	Shrub dist.	Shrub height	Distance to neighbor	Slope
1 (14)	5.7^{a} 3.1	5.5^{a} 1.4	1.4 0.8	0.22^{a} 0.08	6.1 11.0	12.8^{c} 2.3
2 (18)	9.6^{b} 3.4	2.8^{b} 1.4	1.5 0.7	0.34^{b} 0.11	4.4 5.4	3.7^{a} 1.0
3 (5)	8.7^{ab} 4.1	3.3^{ab} 2.8	1.9 2.7	0.28^{ab} 0.07	6.0 1.9	6.0^{b} 2.1
4 (5)	6.1^{a} 1.9	13.3 7.1	0.6 0.2	0.29^{ab} 0.08	4.4 4.0	11.1^{c} 0.1

Population Dynamics:

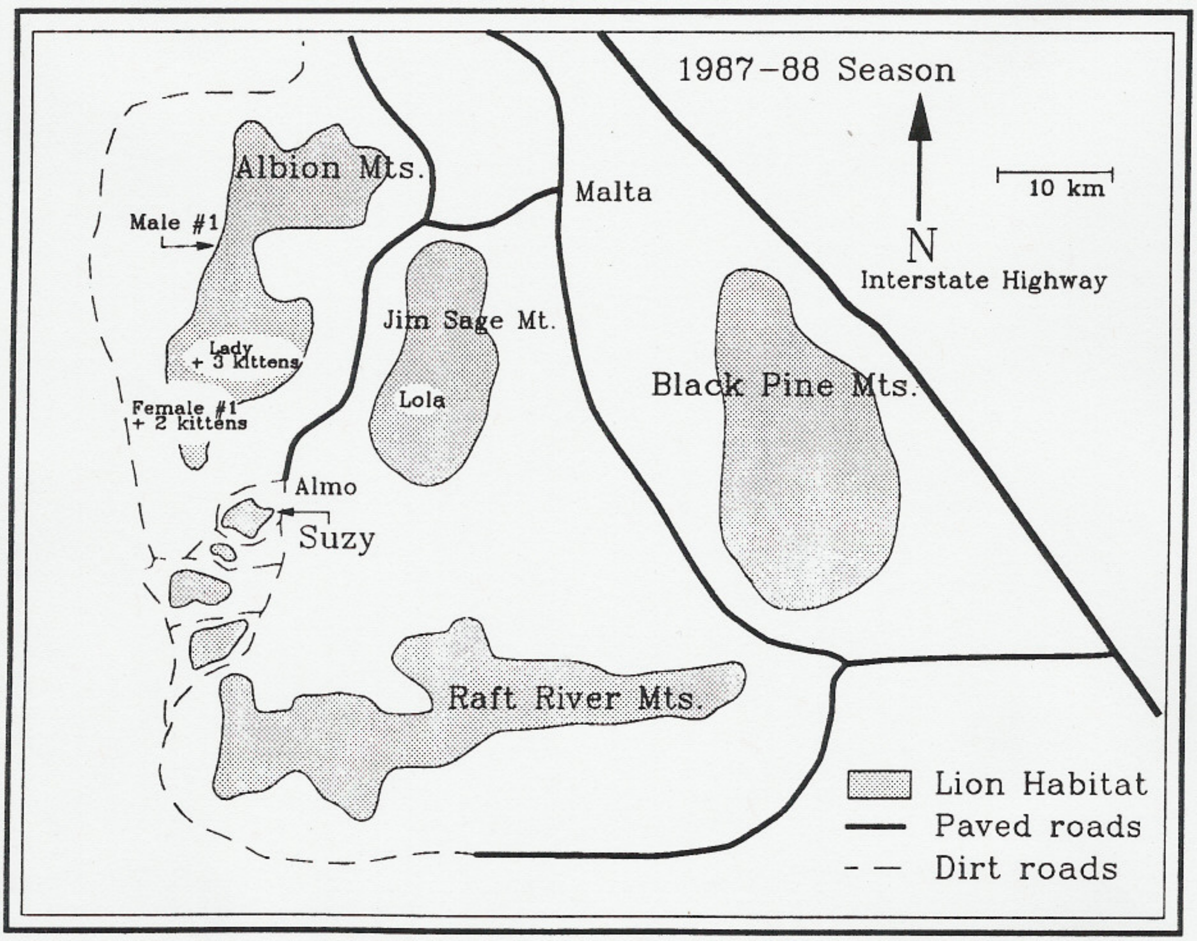
Figure 7 presents data on lions captured or known to be present on much of the study area. One lion, a subadult female, "Lady" was radio-collared the first year of field work (1986-87). This animal was monitored through the summer of 1987 when she lost the transmitter from her collar. The collar remained on her and there were reports of her on the study area in the winter of 1987-88 when she reportedly had three kittens. However, she did not show up on the study area in future winters and was assumed to have emigrated or died. In the second winter field season

Figure 7. Summary of lions captured or known to be present in the study area for the different years of the study. For adult animals, it was assumed that they were present on the area from birth.



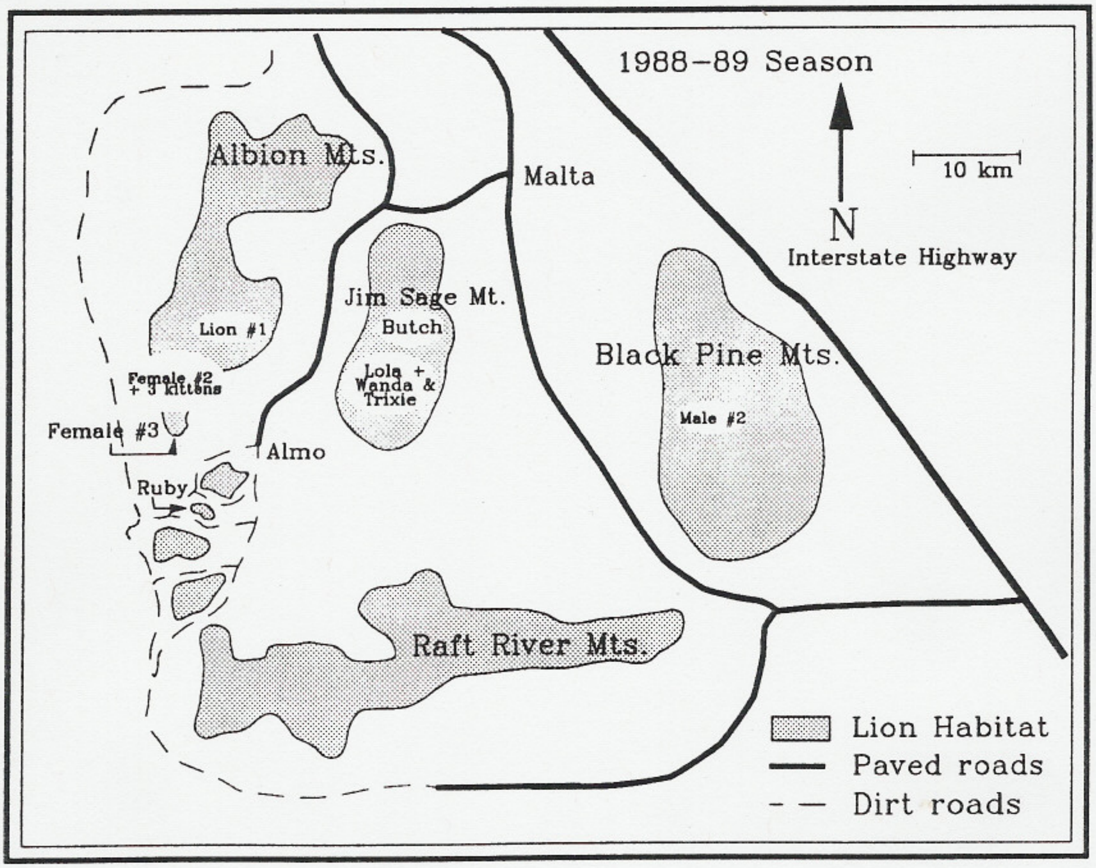
(1987-88), two female lions (Lola and Suzy) were treed and radio-collared (Fig. 7). A third cat, a male, was treed by a local houndsman and reported to the us. Tracks of a female (Female #1) with two kittens were found in the study area (Fig. 8). The collared subadult female (Suzy) was monitored for a month after she was collared and then the signal disappeared. It is speculated that this lion did not leave the area, nor that the collar failed but that the cat was illegally killed.

Figure 8. Locations of the lions captured or known to be in the study area, based on sign, for the winter of 1987-88.



In 1988-89, the adult female Lola was recaptured and recollared along with two kittens she gave birth to during the previous summer (Fig. 9). This female lost her collar when she it hooked on a fence and tore it off in late summer 1989. We did not recapture this female until the winter of 1990-91. At that time she had three small kittens. A week after we re-collared her, she was killed illegally. We found one of her kittens subsequently killed by another lion, presumably a male. It is assumed the other kittens were also killed or died from starvation. In April, 1989, the one collared kitten (Wanda) of Lola was found dead. Tracks near the carcass led

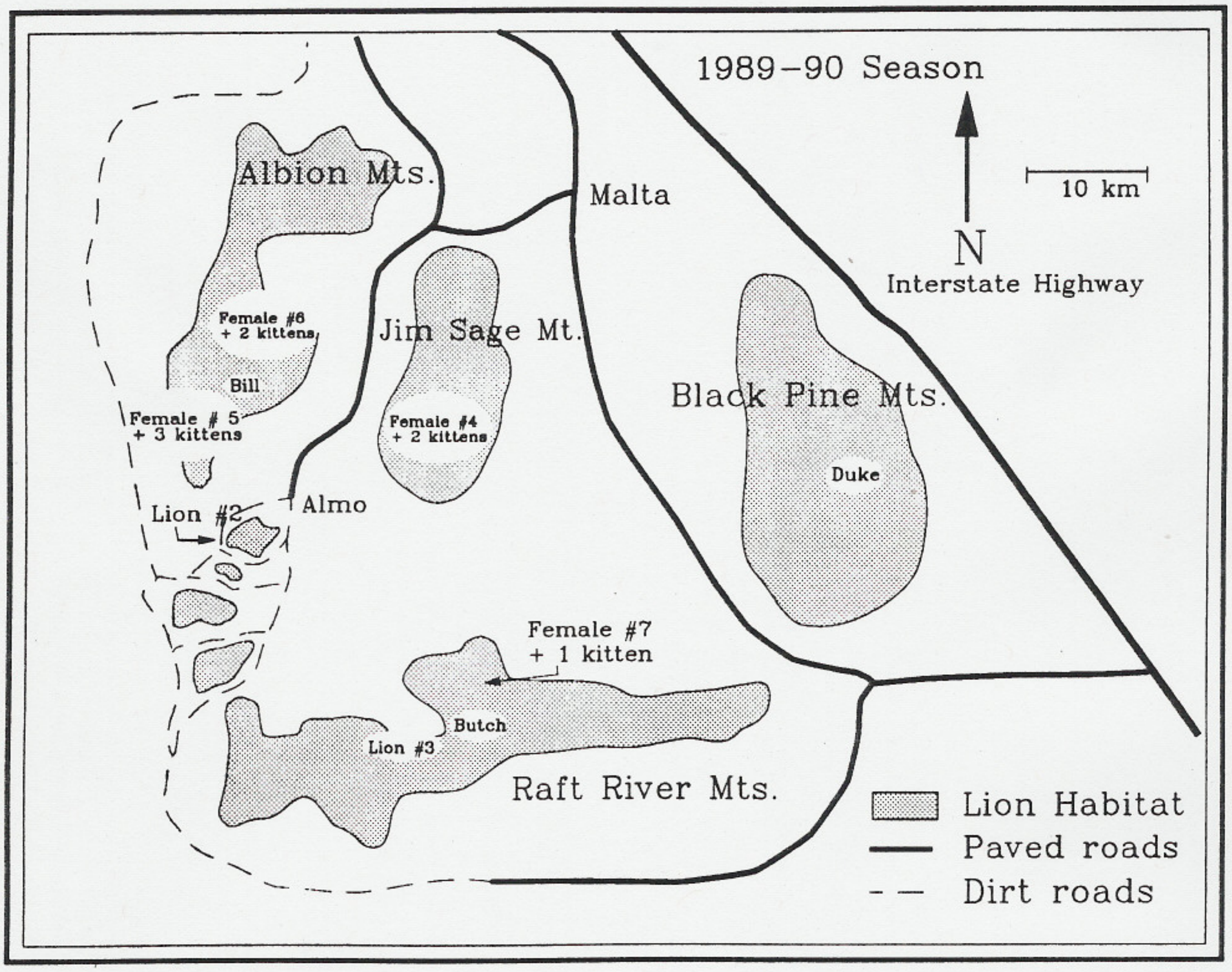
Figure 9. Locations of lions captured or known to be in the study area, based on sign, for the winter of 1988-89.



to the capture of a large adult male (Butch). It was assumed this lion killed the collared kitten and likely her sister (Trixie). The male cat was collared and released. A local houndsman chased another female (Female #2) with three small kittens in 1988-89 (Fig 9). One of the kittens was killed by the dogs at that time. Another subadult female (Female #3) was caught in a local trapper's trap but escaped when the trapper approached. Tracks of another lion (Lion #1) of unknown sex were also found on the study area (Fig. 9). These tracks were large and likely represent an adult. An adult male (4-5 years old) was harvested in winter 1988-89 in the Black Pine mountains (Fig. 9) and reported to Idaho Fish and Game Department. For 1988-89, sign of 12 lions (7 adults, 5 kittens) were found but certain areas, such as the north side of Raft River Range and Black Pine Range, were not surveyed adequately.

In the winter of 1989-90, a young male lion (Duke) was captured and collared in the Black Pine Mountains and another male (Bill) was captured and collared near the City of Rocks (Fig. 10). The male captured the previous winter (Butch) was killed by a hunter in Utah in late winter. Duke emigrated from the area to a range 100 km to the east where he was harvested legally in the fall of 1991. In 1989-90 all of the study area was surveyed for lion sign. Tracks of a female (#4) and two kittens were found in the central part of the range (Fig. 10). Tracks of another female (Female #5) and two kittens were found in the Jim Sage Mountains (Fig. 10). One of the kittens (Spike) was treed but was too small to fit with a radio collar. This lion was eartagged and released. We were unable to relocate the female and kittens later. Tracks of a female (Female #6) and three kittens were found in late winter (Fig. 10) in the City of Rocks but were not captured. Another female (Female #7) with one kitten were treed in Utah by houndsmen and reported to us. Tracks of two other lions (Lion #2 and Lion #3) were also located (Fig. 10). Definite sign was found for 16 lions (8 adults, 8 kittens) on the study area during the 89-90 winter.

Figure 10. Locations of lions captured or known to be in the study area, based on sign, for the winter of 1989-90.



Reproduction and Recruitment:

Reproduction in the City of Rocks and Jim Sage sections of the study area from 1987 to 1990 included five kittens in 87-88, five kittens in 88-89, and five-seven kittens in 89-90. Our first estimate of reproduction in the north side of the Raft River Range was one kitten in 1989-90. Although five-seven kittens seem to be produced per year in the Idaho section of the study area, recruitment is quite low. Of the five kittens born in 87-88, only two showed up as sub adults the next winter. One of those, Ruby, was likely killed illegally that winter. The other animal could be still in the area. Of the five kittens born in 1988, three died, one was killed by a houndsman's dog and two (Wanda and Trixie) were killed by a male lion (Butch). The other two may still have been alive and with their mother in 1990.

DISCUSSION

Home range characteristics

To date, we have data on home range size for four mountain lions (two females and two males). This number is insufficient to draw definite conclusions on home range size. What is evident at this time is that home range size is quite variable. Home range size is dependent on the quality of habitat the individual has available. Quality, in turn, depends on how well an area supplies food, shelter, and other necessities for living. For mountain lions in our study area, home range size will depend on how well an individual mountain range supplies these requirements. For example, based on our findings, the Jim Sage range was sufficient for an adult female but not an adult male. Subsequently, the male's home range encompassed portions of two other mountain ranges. This use resulted in a substantially larger home range size compared to the female and to the second male. The home range pattern for the first male also demonstrated the importance of corridors linking mountain ranges together. For the second male, habitat quality within his much smaller area of use evidently was sufficient to supply his requirements. To determine if lions are using similar amounts of equal quality habitat, future estimates of home range size will be adjusted based on habitat quality, as determined from home range use and predator-prey patterns.

Activity

Based on our limited findings to date, daily activity patterns of mountain lions emulate the typical crepuscular pattern of most wildlife. As with other species, there is some "noise" inherent in the pattern as individuals make adjustments to situations that may arise, e.g. avoidance of mid-day heat or mid-night cold. Relative to the two methods of comparing activity levels, pulse change rates are probably more indicative of the type of movements being made and the type of terrain being traversed than to actual distance being traveled. Lions seemingly make many short movements (<50 m) that may not be detectable based on relocation data; pulse change rates may be a better assessment of these types of activity. More work, however, is needed to "calibrate" our system so that types of activity can be ascertained from the data. To accomplish this, we will collar a "pet" mountain lion and video tape its activity. Movements made by the lion can then be "fingerprinted" and compared to the type of activity we are seeing in the field.

Conspecific interactions

It has been inferred that wild female mountain lions which lose their kittens come into estrus soon after the loss occurs (Hornocker 1969, Seidensticker et. al 1973). This phenomenon has been documented in captive populations (Eaton and Velander 1977). However, it has not been documented in the wild. Butch killed Lola's kittens the first of April 1989. We believe Butch and Lola mated during the end of April and that Spike was one of their offspring. Also, mutual avoidance (Hornocker 1969 and Seidensticker et. al 1973) between Lola and an unknown lion in January 1989 and Lola and Butch in June 1989 occurred during this study.

Predator-prey interactions

Our data base on lion predation is still insufficient to draw conclusions concerning trends in prey selection by lions. All segments of the deer population are represented in the sample. This preliminary finding supports those of Hornocker (1970). We will continue to locate additional kill sites and substantially increase our sample size to determine if this pattern continues.

At this time, our data on the habitat characteristics at kill and bed sites is insufficient to determine if habitat influences lion hunting success or bed selection by deer. We have measured vegetative characteristics around the sites and will be comparing these data to those from kill and bed sites. These future comparisons should provide further insight into habitat selection with regards to predator-prey interactions.

Population Dynamics

Estimates of lions present were not considered to be reliable for the first year of the study. However, reliable estimates of minimum number of lions in much of the study area were made for the winters of 1987-88, 1988-89, and 1989-90 with the best estimate being for the last winter (89-90). During that winter, extensive surveys were made in all parts of the study area, except for the Black Pine Range.

In estimating minimum numbers of lions in the study area for the previous winters, it is necessary to consider which tracks seen in different winters but in the same area may represent the same lion. Before estimates of minimum numbers of lions in study area can be made, possible overlaps must be considered. For the Jim Sage Mountains, tracks of Female #4 (Spike's mother) found in the Jim sage mountains in 1989-90 were likely those of Lola. Thus only one resident female likely lived there. Based on the movements of Butch, a male lion will spend extended periods of time in a range but can also use other ranges in the area. For the north side of the Raft River range in Utah, we only have reliable data for 1989-90. Based on our data for 1989-90, three adult lions (one female, one male, and one of unknown sex) used that range. However, one of those lions, Butch, also used the Jim Sage range in Idaho. For the City of Rocks area, our estimate of lion density for 1989-90 include one adult male (Bill), a female with three kittens (Female #5), a female with two kittens (Female #6), and one adult lion of unknown sex (Lion #2) (Fig. 10). We just initiated search efforts in the Black Pine Mountains in 1989-90 and except for the capture of the two year old male (Duke), did not do a reliable survey of the area.

Based on estimated ages of captured animals and minimal ages of lions located by tracks, reliable estimates of minimum numbers of lions in various parts of the study area could be made for winters prior to 1989-90. However, as before, possible replicates must be considered. For the winter of 1988-89, data (Fig. 9) indicate only one resident female (Lola) with two kittens (Wanda and Trixie) were in the Jim Sage range. For the City of Rocks area, Female # 2 could be the same animal as Female # 5 or Female # 6 from 1989-90 (Fig. 10). Female's # 2 and 5 were likely not the same lion, if they were, the kittens with female #5 in 89-90 could not be the same ones found with her in 88-89; there would only be two and they would be approximately one year old. The kittens of Female #5 in 89-90 were only about 6-9 months old, based on the size of their tracks. It is more likely Females #2, and 6 are the same animal. Based on track size, the kittens of Female #6 in 89-90 could be the approximate age of Female # 2's kittens from 88-89. The tracks of Lion #1 found near the Castles in 1988-89 (Fig. 9) could have been those of the male lion captured in the same area in 89-90 (Bill). Female # 3 (Fig. 9) could be the same as lion # 2 whose track was found in 1989-90 (Fig. 10). Taking these possible duplications in consideration, the lion population in the City of Rocks area for 1988-89 includes two females with kittens, two subadult females (Ruby and Female # 3) and one adult male (Bill).

For the winter of 87-88 in the City of Rocks area, Ruby and Female# 3 from 88-89 were possibly kittens of Female #1 in 87-88 (Fig. 8) or of the collared female Lady. Ruby was approximately 12-14 months old when she was captured and the trapped female was of similar size. Based on the track size, the kittens of Female #1 were about 4-6 months old the winter of 87-88, that would make them 16-18 months old in 88-89. Lady's kittens were only 1-3 months old in 87-88, making them 13-15 months old in 88-89. Given the uncertainty of the kittens ages in 87-88, it is unknown which could represent Ruby and Female #3. Females # 5 and 6 from 89-90 (Fig. 9) could represent female # 1 and Lady from 1987-88 (Fig. 8). Based on this analysis, it is estimated that two females with kittens, one sub adult female (Suzy) and one male occupied the City of Rocks area in 1987-88. Our survey effort from the Jim Sage range was not intense enough to make an estimate of lion numbers for 87-88. However, One female, Lola, was captured there that winter. This lion did not have any kittens with her, nor was she pregnant. She did have two kittens (Wanda and Trixie) later that summer so at some time, a male lion had to at least temporarily inhabit the Jim Sage Range that summer. It is unknown if this animal was Butch. DNA analyses are being made of tissue samples of Butch and Wanda to determine if they were related.

In summary, the most reliable population estimate for the study area was made for the 1989-90 season. Based on those data, a total population estimate of the study area, excluding the Black Pine Mountains and the south side of the Raft river range, would be eight adult lions (two males, four females, two unknown sex) and eight kittens. The population estimates for 1987-88 (seven adults and five kittens) and 88-89 (six adults and 5 kittens) are not considered as reliable as for 89-90 but are similar in magnitude.

Reproduction and Recruitment

Based on the data, approximately 5-7 kittens were born in the study area per year. However, few of these kittens showed up as subadults. Ruby and Female #3 could be the kittens of unknown Female #1. Ruby, however, disappeared shortly after she was captured and collared in January 1989. Female # 3 could have been unknown Lion #2 in 89-90.

Management implications:

At this time we cannot make any indepth management recommendations. However, some of our preliminary results may have some management implications if the patterns withstand additional data analysis. It is assumed that lions generally migrate with their main prey, mule deer, to the winter range. The confined use of the home range by two females supports this contention. During winters of extreme snow fall, deer are more concentrated on these winter ranges, thus concentrating the mountain lions and possibly making them more susceptible to hunting pressure. This movement pattern must be taken into consideration in future regulations to guard against over harvest during winters of extreme snowfall. If there is no other limit on the number of lions that can be harvested, perhaps a harvest season tied to snow fall depth might be an appropriate strategy. Once snow fall reached a minimum depth, regulations limiting the number of lions to be taken or closure to pursuit only could protect the population from overharvest.

In fragmented habitat it is crucial that corridors between usable habitat patches be identified and protected from development. Through our observations of Butch as as well as observations by local ranchers and trappers, we have identified at least two corridors. One connecting the Raft River range and the Jim Sage Mountains. The second one linking the Albion Mountains with the Jim Sage. Butch used both corridors often. If barriers were placed in these corridors it would essentially seal off dispersal into the Jim Sage Mountains. The Jim Sage Mountains are probably too small to contain a breeding population of mountain lions without these corridors. Management of lions in areas like the Jim Sage range should include identification of the corridors necessary to maintain viable populations. Part of our future goals is to determine if likely corridors between ranges can be identified based on habitat characteristics within and between the ranges.

Interactions noted between Lola and her kitten, Wanda, may also indicate significant management problems. Current hunting regulations state that hunters may not shoot females with kittens. Since the mother may only be with her kittens fifty percent of the time, hunters must be extremely careful when determining the sex and reproductive status of any treed lion. Since it is probably impossible to eliminate the orphaning of kittens, any viable management plan will have to provide for kitten mortality.

Relative to the current lion population in the core of our study area, our work indicates that there is a very limited number of lions there. We have also found that a majority of the mortality on the population is human induced. It is thought that the study area could support substantially more lions than what occurs now but that the human induced mortality is keeping the population below a recoverable level.

The validity of these contentions could be tested by closing the study population to legal hunting pressure and reducing the illegal harvest. Such action would enable us to determine what the recovery rate of the population was and, as importantly, determine the maximum number of lions the area could support. These data would help resource managers in Idaho and Utah to determine future sustainable harvest levels.

FUTURE RESEARCH PLANS AND EXPECTED RESULTS

To date, the main objective of our study was to collect baseline data on mountain lions in fragmented habitat. Our progress so far and our anticipated future progress will provide the data necessary to meet this objective. However, in conjunction with our original objective, the data we are collecting affords a unique opportunity to test various theoretical models in population genetics, behavior, and ecology that would be beneficial to managing lions and potentially other predators, in fragmented habitat. Thus, the objectives of our future field work will focus on testing several theoretical models as they may pertain to our study population.

Three theoretical concepts were chosen for testing: 1) impact or cost of inbreeding, 2) evolutionary causes and population effects of infanticide, and 3) optimum foraging strategies. These three were chosen because of the lack of data in these areas and of their potential importance to conservation biology (Ralls et al. 1988, Soule' and Kohm 1989).

Populations of mountain lions are small even under ideal conditions. In fragmented habitat, population numbers are further reduced which, coupled with isolating mechanisms, result in extremely small effective population sizes with high rates of inbreeding. Maintenance of mountain lions in areas of fragmented habitat then, could be severely hindered by inbreeding and inbreeding depression (Ralls et al. 1988, Soule' and Kohm 1989). The conservation of mountain lions therefore could be dependent on predicting the "cost of inbreeding" (Ralls et al. 1988).

The cost of inbreeding for our population will be estimated based on the equations in (1) (Ralls et al. 1988). These equations were chosen because of their current use in determining the cost of inbreeding in mammal populations. The first equation (1a) is the log transformed model for estimating the proportion of individuals surviving to a target age (S). The target age for our study will be one year. The parameter A is a measure of mortality in a randomly mating population and B is a measure of the rate at which survival decreases as inbreeding increases. The second equation (1b) estimates the cost of inbreeding (i) based on values of B and the inbreeding coefficient (F_x).

(1)

$^{a}\ \ln S = A + F_x B$ $\qquad$ $^{b}\ i = 1 - e^{-F(x)B}$

From data on population dynamics we will generate estimates of survival rates (S). The measure of death from a randomly mating population (A) can be estimated from literature values from lions in unfragmented areas (Hemker et al. 1984, Hornocker 1969, Lindzey et al. 1988). In a review of the existing data, Ralls et al.

(1986) found no evidence of extensive inbreeding in large unconstrained populations. Thus inbreeding in lions from unfragmented areas can be presumed low and mortality levels of these populations can be used as an estimate of A. The value of (B) (Ralls et al. 1988) is then estimated by 1a and the cost of inbreeding (i) by 1b.

Infanticide in mountain lions has been reported by several authors (Hornocker 1970, Robinette et al. 1961, Young 1927) and one incident has been documented in the present study. Male initiated infanticide is reportedly common in large mammalian predators (Packer and Pusey 1984). Packer and Pusey (1984) summarized the current state of knowledge of infanticide and concluded the practice imparted some reproductive advantage for male African lions (*Panthera leo*). However, little is known of the reasons for male initiated infanticide in other large, mostly solitary, predators such as mountain lions. Determination of the causative factors for male initiated infanticide in mountain lions is critical to calculating this practice's impact on the population dynamics of these species, especially in fragmented conditions, and to maintaining viable population sizes.

In the study area, there are a minimum of four known male territories each encompassing approximately 3-4 female home ranges. The population is currently hunted so periodic removal of resident male lions is anticipated. Consequently, residence time of territorial males is variable. To date, one male retained his territory for only one year before he was harvested by hunters. Another male has been resident in the same territory for approximately 3 years. Thus over the proposed length of the study, each of the four male territories will likely have different male residence times. Rates and initiators of infanticide in each territorial area will be determined from the telemetry data. The paternity of the infanticidal male to the killed kittens will be determined by DNA fingerprinting. These data will be compared to critically test the theory of infanticide being an evolutionary strategy by new males when taking over vacated male territories.

The documentation of infanticide rates will also be used to determine the impact of such a practice, under fragmented conditions, on overall survival and recruitment rates. If infanticide is primarily by takeover males, survival rates of kittens in territories with shorter male residence times should be significantly lower. Reproduction and survival data for females within each territory, available from capture and telemetry data, will be compared.

Optimum foraging theory (Charnov 1976, Emlen 1966, MacArthur and Pianka 1966) attempts to explain and predict strategies animals use in selecting food types, moving from one food source (patch) to another, and using various food patches available. Of these three general areas of optimum foraging strategies, movement to and from and use of patches are most germane to lions in fragmented habitat. How patch size, geometry, composition, and distribution are perceived by an animal and influence its use of those patches ultimately determines the impact fragmentation has on the species. Factors such as minimum critical habitat size, fragment distribution, and corridor size and location are all direct functions of the decisions individuals make regarding habitat use. If optimum foraging theory can be used to explain and predict the dynamics of habitat use it could become a useful tool in conserving lion populations in fragmented environments.

Optimum foraging models makes several general qualitative predictions relative to patch use. Animals should spend more time in "good" or high quality patches, they should obtain more energy yield from these patches, and residence time and patch yield should increase as travel time between patches increases (McNair 1982). For mountain lions' use of a patchy habitat, optimum foraging predicts lions should spend more time and be more successful in larger or higher quality habitat patches where their food (mule deer) are most likely to be found, are most vulnerable, or are less likely to leave the patch (lower depletion rate). From this, optimum foraging theory would predict three possible use patterns relative to residence time in individual food patches. Average weighted time spent in large food patches should be statistically greater than average time spent in smaller ones, provided travel time is constant. Secondly, for patches of equal quality, residence time should be determined mainly by travel times between patches. There should be higher residence times in patches with greater travel time to the next patch. Thirdly, residence times for patches of unequal quality and unequal travel times should be positively correlated with patch quality and negatively correlated with travel time.

The condition to test the general hypotheses of equal travel time but unequal patch quality (Prediction # 1) is met in the study area for food patches within a mountain range. Travel times between food patches can be considered minimal and thus constant because of the small range size and the mobility of the lions. The percent time lions stay in habitat patches should statistically correlate with patch size or quality. Likewise, the number of kill sites, an indicator of yield, should be higher, than expected by proportional chance, in larger patches.

For patches of equal quality, residence time should be determined mainly by travel times between patches (Prediction # 2). Because of increased travel time, inter-range movements between patches of equal quality should be less frequent than for movements between intra range patches. Thus, average residence time in a patch before an intra range movement to an equal quality patch should be less than residence times before an inter range movement. Lions should spend more time in a habitat patch before deciding to move to another range than they would in deciding to move to a patch within the same range. Residence times, as determined by radio-telemetry, prior to intra range verses inter range patch movements will be compared. The null hypothesis tested would be no difference in residence times in patches used before intra and inter-range movements.

Lastly, the combined impact of patch quality and travel time (Prediction # 3) can be tested as follows. Each mountain range in the study area differs in size, distance from adjacent ranges (Fig. 2), and in the number of food patches or quality. Consequently each range can be considered a food patch with a unique nondepletable food value. Optimum foraging theory would predict lions should have longer residence times on the larger or more complex (higher value) ranges. Residence time on a given range should also be shorter before a move to a larger range than it should be before a move to a smaller one.

Results of this study in the three areas outlined would increase our understanding of fundamental ecological principles as they pertain to mountain lions. The proposed work would also further the application of several theoretical concepts to the conservation management of mountain lions in fragmented habitat.

Although the emphasis of the study will be changing in the coming years, actual data collection will be similar to previous years. Collection of data on home range use patterns will continue as before with the help of volunteers from the Earthwatch organization. These data, however, will be used to address questions concerning optimum foraging. Testing of optimal foraging models proposed requires determining which habitat types are considered food patches and then estimating their quality. The study area consists of approximately 4-5 recognizable habitat types of varying size and shape. Based on preliminary findings from this work and data from others (Belden et al. 1988), lions do not use all habitat types proportionally the same. Additionally, predation success in lions varies with habitat type (Hornocker 1970). Consequently, it is assumed the differences in habitat use by lions reflects dissimilar food values of the various habitat types. The value of a habitat type as a food patch for lions can be considered a function of the amount of time lions spend in that habitat type and the ease of catching deer by lions within the habitat.

The relative use of each habitat type by lions can be estimated by monitoring habitat use patterns of radio marked animals. Relative time marked individuals spend in different habitat types will give estimates of use patterns for each type. Location and habitat assessment of sites of successful predation by lions should give estimates of deer vulnerability for different habitat types.

The vegetation data from kill sites and general areas will be used to quantify habitat characteristics of "food" patches. The number of kill sites within each habitat type, standardized for the relative amounts of each type, will be used as an index of prey susceptibility per habitat type.

To test the predictions made, data on how individual lions use the food patches within their home range on a spatial and a temporal basis are needed. The telemetry data collected on lions will be used to estimate lions' residence time within a habitat patch and travel time between patches. The time an animal enters and then leaves a patch, as determined by triangulation, can be calculated. The difference between the two times yields residence time. Travel time between patches would be the difference in time between a lion leaving a patch and arriving at another.

The data on population dynamics from our winter capture efforts can be used to test the impact of inbreeding and infanticide on the lion population. With the added help of the Earthwatch organization we are planning on increasing our winter field work significantly. This added effort should provide us with the population dynamics data necessary to test the proposed theories in inbreeding and infanticide.

The blood samples we collect from the lions we capture will also be used to test hypotheses in inbreeding and infanticide. These blood samples will enable us to determine the genetic relationships of the lions in the study area. For inbreeding, an inbreeding coefficient (F_x) for the population will be calculated by the pedigree method (Ballou 1983). Briefly, this method involves drawing a pedigree chart for each individual, looking for connecting paths from an individual through one parent to a common ancestor to the other parent. These common ancestral steps (i) are summed and the inbreeding coefficient (F_x) is equal to $1/2^{i-1}$. Relative to infanticide, the genetic relationships will help determine whether the kittens males kill are related to them or not.

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Literature Cited

Ballou, J. 1983. Calculating inbreeding coefficients from pedigrees. Pp 509-520 *in* C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and W. L. Thomas, eds. Genetics and conservation: A reference for Managing Wild Animal and Plant Populations. Benjamin/Cummings, Menlo Park, CA.

Belden, R.C., W.B. Frankenberger, R.T. McBride, and S.T. Schwikert. 1988. Panther habitat use in southern Florida. J. Wildl. Manage. 52:660-663.

Brower, J.E. and J.H. Zar. 1977. Field and laboratory methods for general ecology. W.C. Brown, Dubuque, IA.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. Theor. Pop. Biol. 9:129-136.

Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. New York State Conserv. 3:19-22.

Eaton, R.L. and K.A. Velander. 1977. Reproduction in the puma: biology, behavior, and ontogeny. Worlds Cats. 3:45-70.

Emlen, J.M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.

Hemker, T.P., F.G. Lindzey, and B.B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. J. Wildl. Manage. 48:1275-1284.

Hornocker, M. G. 1969. Winter territoriality in mountain lions. J. Wildl. Manage. 33:457-464.

Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monog. #21.

Laundre', J.W., T.D. Reynolds, S.T. Knick, and I.J. Ball. 1987. Accuracy of daily point relocations in assessing real movements of radio-marked animals. J. Wildl. Manage. 51:937-940.

Lindzey, F.G., B.B. Ackerman, D. Barnhurst, and T.P. Hemker. 1988. Survival rates of mountain lions in southern Utah. J. Wildl. Manage. 52:664-667.

MacArthur, R.H. and E.R. Pianka 1966. On optimal use of a patchy environment. Amer. Nat. 100:603-609.

MacDonald, D. W., G. Ball, and N. G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. Pp. 405-424 In C. J. Amlander and D.W. MacDonald, eds. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford, England. 804 pp.

McNair, J.N. 1982. Optimal giving-up times and marginal value theorem. Amer. Nat. 119:511-529.

Neal, D. L. G. N. Steger and R. C. Bertram 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. Res. Note PSW-392. Berkeley, CA: Pacific southwest Forest Service, U.S. Dept. of Ag. 6pp.

Packer C. and A.E. Pusey. 1984. Infanticide in carnivores. pp 31-42 *in* G. Hausfater and S.B. Hrdy, eds, Infanticide Comparative and Evolutionary Perspectives, Aldine Pub. New York.

Ralls, K., P.H. Harvey, and A.M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pp 35-56 *in* M. Soule', ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, MA

Ralls, K., J.D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conser. Biol. 2:185-193.

Robinette, W.L., J.S. Gashwiler, and O.W. Morris. 1961. Notes on cougar productivity and life history. J. Mammal. 42:204-217.

Rongstad, O.J. and J.R. Tester. 1969. Movements and habitat use of white-tailed deer in Minnesota. J. Wild. Manage. 33:366-379.

Russell, K. R. 1978. Mountain lion. pages 207-225 in J. L. Scmidt and D. L. Gilbert, eds. Big game of North America: ecology and management. Stackpole Co., Harrisburg, PA 494 pp.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildl. Monog. 35:1-60.

Shaw, H. G. 1983. A mountain lion field guide. Arizona Game and Fish Dept. Sp. Rep. No. 9. 27 pp.

Soule', M.E. and K.A. Kohm. 1989. Research Priorities for Conservation Biology. Island Press, Washington, D.C.

Thomas, D.C. and P.J. Bandy. 1973. Age determination of wild black-tailed deer from dental annulations. J. Wildl. Manage. 37:232-235.

Verme, L.J. and J.C. Holland. 1973. Reagent-dry assay of marrow fat in white-tailed deer. J. Wildl. Manage. 37:103-105.

Whitfield, M.B. 1983. Bighorn sheep history, distributions, and habitat relationships in the Teton Mountain Range, Wyoming. M.S. Thesis, Idaho State Univer., Pocatello. 244pp.

Young, S.P. 1927. Mountain lion eats its kittens. J. Mammal. 8:158-160.

Young S. P. and E. A. Goldman 1946. The puma, mysterious American cat. The Am. Wildl. Inst., Washington D.C. 358 pp.